

ORIGINAL ARTICLE



Cape (*Apis mellifera capensis*) and European (*Apis mellifera*) honey bee guard age and duration of guarding small hive beetles (*Aethina tumida*)

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SUMMARY

The guard age and duration of European (*Apis mellifera*) and Cape (*A. m. capensis*) honey bees guarding small hive beetles (*Aethina tumida*) were determined using 3-frame observation hives, noting the commencement and termination of beetle guarding by individually labelled honey bees. European honey bees in the USA began guarding small hive beetles significantly earlier (beginning age 18.55 ± 0.52 days; mean \pm s.e.), guarded beetles significantly longer (duration 2.36 ± 0.31 days), and stopped guarding beetles significantly sooner (ending age 19.91 ± 0.57 days) than Cape honey bees in South Africa (beginning age 20.61 ± 0.38 days; duration 1.43 ± 0.12 days; and ending age 21.04 ± 0.37 days). Although the timing of beetle guarding behaviour between the two subspecies is significantly different, it does not explain the differential damage to European and Cape honey bee colonies caused by small hive beetles.

Keywords: *Apis mellifera*, *Apis mellifera capensis*, *Aethina tumida*, guarding behaviour, guard age, small hive beetle, Cape honey bees, age-related division of labour

INTRODUCTION

Small hive beetles (*Aethina tumida*) are scavengers of honey bee (*Apis mellifera*) colonies. They are native to sub-Saharan Africa (Hepburn & Radloff, 1998), where their populations usually are controlled by defensive behaviour of their honey bee hosts (Elzen *et al.*, 2001; Neumann *et al.*, 2001). In contrast, small hive beetle infestations in colonies of European-derived *A. mellifera* subspecies are often extremely damaging to host colonies in the United States (Elzen *et al.*, 1999; Hood, 2000). This occurs despite European bee defensive behaviour that appears to be qualitatively (but not necessarily quantitatively) similar to that of African honey bees (Ellis, 2002).

In addition to direct aggressive behaviour (biting, stinging) directed at small hive beetles (Elzen *et al.*, 2001), African honey bees construct propolis prisons in which small hive beetles are encapsulated (Neumann *et al.*, 2001). Similar imprisoning behaviour has been documented in European honey bees (Ellis, 2002) but the efficacy of social encapsulation by European honey bees remains unknown. Regardless, both honey bee subspecies station guards, who keep the beetles imprisoned, around the prison perimeter (Neumann *et al.*, 2001; Ellis, 2002) (fig. 1). Despite being imprisoned, small hive beetles are able to remain alive because they are fed by their honey bee captors (Ellis *et al.*, 2002).

In this study, we determine the age of European and Cape (*A. m. capensis*) honey bees that guard small hive beetles and the duration of beetle guarding for each honey bee subspecies. These data show guarding differences between the subspecies, suggesting possible reasons why African honey bee subspecies can cope with small hive beetle infestations while European honey



FIG. 1. Two European honey bees (one labelled 'yellow 71') guarding an imprisoned small hive beetle. Notice the ridge of propolis, forming a prison wall, at the bottom of the photograph.

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TABLE 1. Beginning guard age, ending guard age and duration of guarding behaviour (days) for Cape and European honey bees guarding small hive beetles. The two bee subspecies differed for each parameter at $P \leq 0.05$.

Guarding	Cape honey bees mean \pm s.e. (n)	European honey bees mean \pm s.e. (n)
Average beginning guard age	20.61 \pm 0.38 (49)a	18.55 \pm 0.52 (33)b
Average ending guard age	21.04 \pm 0.37 (49)a	19.91 \pm 0.57 (33)b
Average duration of guarding behaviour	1.43 \pm 0.12 (49)a	2.36 \pm 0.31 (33)b

TABLE 2. Location \times colony interactions for average beginning guard age and ending guard age (days) of Cape and European honey bees guarding small hive beetles. Because of the significant interaction, colony analyses were run separately by location for these variables. Row totals followed by the same letter are not different at the $\alpha \leq 0.05$ level. Means were separated using ANOVA's and Tukey's multiple range tests.

Cape honey bees	colony 1 mean \pm s.e. (n)	colony 2 mean \pm s.e. (n)	colony 3 mean \pm s.e. (n)
Average beginning guard age	22.83 \pm 1.51 (6)a	20.97 \pm 0.36 (29)a	18.93 \pm 0.73 (14)b
Average ending guard age	23.17 \pm 1.45 (6)a	21.59 \pm 0.29 (29)a	19.00 \pm 0.74 (14)b
European honey bees	colony 1 mean \pm s.e. (n)	colony 2 mean \pm s.e. (n)	colony 3 mean \pm s.e. (n)
Average beginning guard age	18.2 \pm 1.71 (5)a	17.65 \pm 0.69 (17)a	20.09 \pm 0.72 (11)a
Average ending guard age	18.2 \pm 1.71 (5)a	19.47 \pm 0.73 (17)a	21.36 \pm 0.93 (11)a

bee subspecies cannot. Furthermore, these data aid in describing the recently discovered phenomenon of propolis prisons that are used by honey bees as a defensive tactic against small hive beetles.

MATERIALS AND METHODS

The experiments were conducted at Rhodes University in Grahamstown, South Africa (January–April and November–December 2001), and in Warren County, Georgia, USA (August/September 2001). In both locations, three observation hives were used. Each hive contained three frames of bees, two frames of brood, one frame of honey, and a laying queen. Honey bees used in the USA were of mixed European origin, while Cape honey bees (*A. m. capensis*) were used in South Africa.

Approximately 25–40 small hive beetles were added to each hive 2–3 days after the observation hives were established. Once small hive beetle imprisoning behaviour was apparent in each hive (Neumann *et al.*, 2001), 150–400 newly emerged honey bees, from a mixture of colonies, were individually marked with coloured, numbered labels (Opalithplättchen) and added to each colony. No two observation hives were given newly emerged bees from the same colony.

Hives were monitored daily at approximately 09.00 h, 14.30 h and 20.00 h. Location of imprisoned small hive beetles and guarding behaviour of marked honey bees (described in South Africa by Neumann *et al.*, 2001 and in the USA by Ellis, 2002) were documented noting the commencement and duration of beetle guarding behaviour (fig. 1). Data were collected until all marked bees had stopped guarding beetles (ranging from 21–28 days).

The beginning age of honey bees guarding beetles, number of days they guarded, and the last day they guarded were analysed by analysis of variance (Statistica, 2001). Colonies were nested within location. When colony and location interacted, analyses were run separately by location. Means were separated using Tukey's multiple range tests; differences were accepted at the $\alpha \leq 0.05$ level.

RESULTS

Beginning guard age

European honey bees began guarding small hive beetles two days earlier than did Cape honey bees ($F = 10.99$; $df = 1, 76$; $P = 0.0014$) (table 1). There were colony \times location interactions for beginning guard age ($F = 4.21$; $df = 4, 76$; $P = 0.0039$). In South Africa, workers in one Cape colony (colony 3) began guarding small hive beetles significantly earlier than in the other two colonies ($F = 6.24$; $df = 2, 46$; $P = 0.0040$; table 2). There were no significant differences with respect to the start of beetle guarding in the European colonies ($F = 2.50$; $df = 2, 30$; $P = 0.099$; table 2).

Ending guard age

European honey bees stopped guarding small hive beetles one day earlier than did Cape honey bees ($F = 5.12$; $df = 1, 76$; $P = 0.027$) (table 1). Colony \times location interactions occurred for this variable ($F = 4.83$; $df = 4, 76$; $P = 0.0016$). Workers in Cape colony 3 stopped guarding beetles earlier than in the other Cape colonies ($F = 9.33$; $df = 2, 46$; $P = 0.00040$) (table 2). There were no significant differences among the European colonies with respect to ending guard age ($F = 2.06$; $df = 2, 30$; $P = 0.15$) (table 2).

Duration of beetle guarding

European honey bees guarded beetles almost one day longer than did Cape honey bees ($F = 4.30$; $df = 1, 76$; $P = 0.041$) (table 1). There was no significant colony \times location interaction for this variable ($F = 2.48$; $df = 4, 76$; $P = 0.051$).

DISCUSSION

European honey bees begin guarding small hive beetles earlier, guard for longer periods of time, and stop guarding sooner than Cape honey bees. This European bee behaviour may be in reaction to damage small hive beetles cause in European colonies (Elzen *et al.*, 1999, 2000; Hood, 2000; Wvenning, 2001; Ellis *et al.*, 2003). Because small hive beetles cause little or no damage in

Cape bee colonies (Ellis *et al.*, 2003), Cape honey bees could be less inclined to begin guarding beetles and then guard for shorter periods of time. This could imply that Cape honey bees are either remarkably efficient at small hive beetle guarding or that there are other factors besides imprisoning techniques that Cape bees use to control small hive beetle infestations. This difference between the bee subspecies could also reflect the differences in aggression towards free-running small hive beetles between African and European honey bee subspecies (Elzen *et al.*, 2001). African workers vigorously attack free-running small hive beetles more often than European workers do. Thus beetle guarding in African colonies may not have to be as efficient.

Furthermore, it is possible that age-related division of labour is different between the two honey bee subspecies, with European honey bees advancing in age-specific tasks faster than their African counterparts. However, division of labour in Cape honey bees is poorly studied and therefore no further inferences on this point can be made.

Interestingly, the commencement of hive entrance guarding behaviour in European honey bees has been documented at 18–19 days of age (Winston, 1992). This is consistent with our findings that European bees began guarding small hive beetles at 18.6 days of age (table 1) which implies that 'guarding' behaviour is the same for honey bees whether they are doing so at the entrance of a hive or entrance of a beetle prison.

Winston (1992) also noted that guarding behaviour in honey bees chronologically overlaps with foraging behaviour, indicating that individuals from the same cohort could be doing either of the two tasks. In this study, labelled honey bees in all colonies in both locations were recorded foraging while other labelled bees were guarding beetles. Therefore, one would expect that if beetle infestations in European honey bee colonies are large, colony foraging activity may be reduced because foraging age bees are guarding beetles instead of foraging. Such reduction in the number of foraging bees for small hive beetle infested European colonies has been documented (Ellis *et al.*, 2003).

African honey bee subspecies south of the Sahara are sympatric with small hive beetles (Lundie, 1940; Schmolke, 1974; Hepburn & Radloff, 1998) and show considerable resistance towards infestations. However, the behavioural mechanisms regulating resistance that have been identified so far (aggression behaviour (Elzen *et al.*, 2001) and prison building (Neumann *et al.*, 2001)) are also present in European bees (Ellis, 2002). This strongly suggests that there are only differences in degree, but not in kind, between Cape and European subspecies with respect to resistance behaviour. Therefore, one could expect that there is some adaptive advantage to the degree of behaviour exhibited by Cape honey bee guards.

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